# TO EAT OR NOT TO EAT?:
# THAT IS THE QUESTION OF TREEFROG PREY SELECTION

By

ARTHUR NELSON FREED

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1982

10 82 2044

ACKNOWLEDGEMENTS

I wish to thank Martha L. Crump and John F. Anderson for the interest and guidance they provided. M.L. Crump, J.F. Anderson, and T.J. Walker kindly reviewed this entire manuscript many times. In addition, P. Feinsinger, R.G. Jaeger, R.A. Merz, R.A. Alford, and Y.B. Linhart critically reviewed various portions of this dissertation. R.A. Alford developed the electivity equation presented in this work. I am grateful to the following people who helped identify particular invertebrates: J. Deisler and G. Goodfriend (Stylommatophora), G.B. Edwards and J. Reiskind (Araneae), D.H. Habeck (Lepidoptera and Coleoptera larvae), R.I. Sailer (Hemiptera), and T.J. Walker (Orthoptera). I thank J. Stevenson of the Florida Department of Natural Resources for permission to conduct this research on Paynes Prairie State Preserve. The work presented here was partially supported by a Sigma Xi Grant-in-Aid of Research and NSF Pre-Doctoral Dissertation Grant DEB-8019502. Finally, I would like to thank my parents for their support and my undergraduate education, which made this dissertation possible.

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS . . . . . ii

ABSTRACT . . . . . iv

OVERVIEW . . . . . 1

SECTION

I A TREEFROG'S MENU: SELECTION FOR AN EVENING'S MEAL . . . . 3

Introduction. . . . . 3
Methods . . . . . 5
Results . . . . . 13
Discussion. . . . . 26

II VISUAL CUES: YOU LOOK GOOD ENOUGH TO EAT . . . . . 30

Introduction. . . . . 30
Methods . . . . . 31
Results . . . . . 33
Discussion. . . . . 43

CRITIQUE: IF I COULD ONLY DO IT OVER AGAIN. . . . . 48

APPENDIX 1 PARAMETER ESTIMATES FOR LENGTH-MASS EQUATIONS. . . . . 51

APPENDIX 2 DIET OF GREEN TREEFROG . . . . . 52

APPENDIX 3 PARAMETER ESTIMATES FOR LENGTH-WIDTH EQUATIONS . . . . . 57

LITERATURE CITED . . . . . 58

BIOGRAPHICAL SKETCH. . . . . 63

Abstract of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

TO EAT OR NOT TO EAT?:
THAT IS THE QUESTION OF TREEFROG PREY SELECTION

By

Arthur Nelson Freed

May 1982

Chairperson: Martha L. Crump
Major Department: Zoology

Frogs have long been considered opportunistic predators. In order to determine if the green treefrog (*Hyla cinerea*) is a non-selective forager, I studied the feeding ecology of this frog on Paynes Prairie State Preserve, Florida, and performed prey selection experiments in the laboratory. The comparison of prey from frog stomachs with prey available in the habitat (determined by tack-trap and sweep netting) indicated that prey selection was not associated with prey availability. Larvae of the families Noctuidae and Cantharidae were the two prey most frequently eaten by *H. cinerea* in the field, but the most common insect families in the habitat were Chloropidae, Cicadellidae, and Entomobryidae. In laboratory preference experiments, the two former prey were ranked highest among the eight natural prey offered to treefrogs. However, the house fly (*Musca domestica*) was consistantly selected over all natural prey. The house

fly was included in these experiments for comparative purposes, since it readily elicits feeding behavior from *H. cinerea* in the laboratory.

Three genus-specific variables influenced prey selection by *Hyla cinerea*: (1) prey length, (2) activity patterns exhibited by prey, and (3) the proportion of time devoted by prey to specific behavior patterns. The quality of feeding stimuli (estimated in captures/h) varied within the behavioral repertoire of a genus as well as among genera performing similar activities. Stimulus quality did not influence the degree or speed of the response exhibited by the treefrog, but only the probability of occurrence of that response. Natural prey items that were consistantly selected in the laboratory possessed length/width ratios greater than 3:1. The average visual angle subtended by prey used by treefrogs as a cue during selection was 2.3° at an average distance of 22.5 cm. Crawling velocity of prey was not an important selection parameter, but tended to be positively associated with the stimulus value of crawling prey.

## OVERVIEW

*Hyla cinerea* is a common green treefrog found throughout the southeastern United States. In north-central Florida green treefrogs are arboreal and at times semi-aquatic. *Hyla cinerea* is a nocturnal, visually oriented, sit-and-wait pursuer (Schoener 1969) that feeds on a variety of invertebrate prey. Foraging begins in the early evening and continues until dawn. During the day, individuals rest in positions concealed by vegetation, or bask (Freed 1980*a*) in exposed positions on grasses and shrubs.

Field work was done on Paynes Prairie State Preserve, located 8 km south of Gainesville, Florida. Hardwood meso-xeric hammock surrounds the study site that consists of three temporary sinkhole ponds adjacent to Alachua Sink. In March, ponds begin drying up, and the area is eventually overgrown by annual plants. Pigweed (*Amaranthus australis*), bagpod (*Sesbania vesicaria*), and sicklepod (*Cassia obtusifolia*) are the most plentiful annuals. Interspersed among these weeds grow several common grasses: coast cockspur (*Echinochloa walteri*), vaseygrass (*Paspalum urvillei*), and guineagrass (*Panicium maximum*).

The vegetation of an area is very important to a treefrog population, since it provides cover, and influences the potential prey available. All invertebrate prey are directly or indirectly associated with these plants. Most of these invertebrates utilize one or more of these plants as food. Stinkbugs (*Euschistus* and *Oebalus*) suck plant jucies whereas caterpillars, flea beetles, and snails (*Spodoptera*,

*Disonycha*, and *Polygyra* respectively) chew or rasp leaves or stems. Those invertebrates that do not rely on plants for food utilize vegetation as foraging areas, and eat herbivorous insects associated with these plants (*e.g. Chauliognathus* and *Clubiona*). Treefrogs are associated with the vegetation in a fashion similar to these predatory invertebrates.

This dissertation addresses the question of prey selection by the green treefrog. The natural diet of the treefrogs found on Paynes Prairie is presented in section one. The food items and their degree of utilization pertain only to this particular population. Other populations occupying nearby habitats may utilize different prey (see Kilby 1945) mainly due to the differences in floral composition of that area. Section one also includes data from laboratory preference experiments designed to determine the degree of prey selectivity exhibited by *H. cinerea*. These laboratory results are compared to data gathered on prey selection under natural conditions.

In section two I examine the potential cues that are used by the green treefrog in selecting prey. Consistent selection of particular invertebrates from a variety of potential prey indicates that treefrogs utilize certain visual cues. In this section I present those cues that are most probably used by *H. cinerea* during prey selection.

SECTION I

# A TREEFROG'S MENU: SELECTION FOR AN EVENING'S MEAL

## Introduction

Pulliam (1974) defined feeding strategy as the choices a predator makes upon encountering different food items, *i.e.*, whether to eat or to ignore a prey. MacArthur and Pianka (1966) presented a model that predicts the optimal diet of a predator based upon the availability of prey species. Later models considered prey availability and also the relative value of the prey to the predator. Emlen (1966), Rapport (1971), Schoener (1971), Cody (1974), Pulliam (1974), Ellis *et al.*, (1976), Estabrook and Dunham (1976), Pyke *et al.*,(1977), Hughes (1979), Sih (1979), and Stenseth and Hansson (1979) defined an optimal diet as one that maximizes energy per unit time. The importance of prey nutrient value to the predator is also recognized (Marten 1973; Pulliam 1975; Rapport 1980). None of these models explains mechanisms allowing for predator discrimination among prey items.

Amphibians in general, and ranids, bufonids, and hylids in particular, are described as indiscriminate predators (Korschgen and Baskett 1963; Johnson and Bury 1965; Klimstra and Myers 1965; Linzey 1967; Heatwole and Heatwole 1968; Hedeen 1972; Kramek 1972; Bury and Martin 1973; Blackith and Speight 1974; Clark 1974; Tyler and Hoestenbach 1979). Oplinger (1967), Johnson and Christiansen (1976), and Labanick (1976), all working on hylids, concluded that availability and abundance of prey rather than preference determine the type of

food consumed by these frogs. Conversely, Cott (1940), Sweetman (1944), Bragg (1957), Turner (1959), Brower and Brower (1962), and Toft (1980) suggested anurans are capable of discrimination among prey. Ingle and McKinley (1978) and Ewert *et al.* (1979) showed that anurans respond differentially to various artificial prey stimuli. I showed that activity patterns of insect prey are differentially utilized as cues in prey selection experiments with *Hyla cinerea* (Freed 1980*b*).

In behavioral studies, both Ewert (1968) and Ingle (1968) reported frogs and toads show consistent size-selectivity in choice of artificial prey. The configuration of a moving stimulus is an important selection parameter (Ewert 1968; Borchers *et al.*, 1978; Ingle and McKinley 1978). Worm-like forms are better feeding stimuli for toads than similarly moving square objects. However, small square stimuli moving in a stepwise fashion elicit stronger feeding responses from toads than squares moving at constant velocity (Borchers *et al.*, 1978). These experimental stimulus movements represent crude simplifications when compared with the diversity and complexity of activity patterns of natural prey (Borchers *et al.*, 1978).

I combined a field study on treefrog feeding ecology with laboratory preference experiments utilizing natural prey. Emphasis was placed on the quality of the behavior patterns exhibited within and among nine prey types. These activity patterns may be used as cues for selection of prey by a foraging predator. The purposes of this study were (1) to identify the prey most frequently eaten by *Hyla cinerea* in the field, (2) to determine the degree to which prey discrimination is developed in the green treefrog, and (3) to estimate the strength of the behavioral cues utilized by the frog during prey selection.

## Methods

Field work on hylid feeding ecology was conducted between May 1977 and May 1978 on Paynes Prairie. Stomach contents of 163 *Hyla cinerea* were obtained via pumping (Legler and Sullivan 1979). Prey abundance was estimated by using Tack Trap® placed on the ground and 0.6, 1.2, and 1.8 m above the ground. Each 315 $cm^2$ plastic sheet of Tack Trap was left overnight or for a 24 h period. Though a significantly greater total number of prey were sampled on ground than aerial traps ($\chi^2 = 518$, df = 18, $P < 0.001$), samples were combined for analysis since family representation at all levels was similar (Spearman Rank Correlation, $r_s = 1$, $P = 0$, N = 8). Sweep net samples were taken between 2100 and 2400 h.

Arthropods were identified to family, and where possible, to genus and species. The rank of prey in the diet of *Hyla cinerea* was determined by calculating the percent biomass-occurrence (*%BO*) for each item:

$$\%BO = \sqrt{\left(\frac{M_i}{M_t} \times 100\right)\left(\frac{N_i}{N_t} \times 100\right)} \quad , \qquad (1)$$

where $M_i$ is the estimated mass of prey $i$, $M_t$ is the estimated mass of all prey items eaten by the sample population, $N_i$ is the number of stomachs containing prey $i$, $N_t$ is the total number of stomachs containing food. The index *%BO* is the geometric mean of two common indicies, % biomass and frequency of occurrence. This compound index determines prey rank based on evenly weighting the potential value of the prey and its frequency of utilization by the predator. It minimizes the effect of extremes in the ranking process, such as abundant tiny prey or

rare large prey, either of which may be insufficient to meet the long term energy requirements of the predator. The length of all whole prey items was measured, and mass estimated by using length-mass regression equations prepared by myself (Appendix 1) or taken from Zug and Zug (1979). The *%BO* was calculated for the most frequently utilized prey genera, and then divided by the summed *%BO* to adjust these values to 100 percent (Table 1).

Thirty-five (18 male, 17 female) *Hyla cinerea* (Snout-Vent-Length: $\bar{X} \pm SE = 4.74 \pm 0.06$ cm, Range= 3.8 - 5.2 cm) were collected during the summer of 1980. They were maintained at room temperature (24°C, light uncontrolled) in the laboratory 1 wk prior to experimentation. The eight top ranked genera of prey as determined by *%BO*, and the house fly (*Musca domestica*), were used as prey for the preference experiments. *Palthus* was omitted from the top eight (Table 2) due to its similarity to *Spodoptera*. The house fly was included for comparative purposes since treefrogs preferred this insect over four mosquito species in laboratory experiments (Freed 1980*b*). The eight prey were divided into two subgroups, each including the house fly. The subgroups were made up of all odd or all even ranked prey as determined by *%BO*. *Clubiona* was switched with *Oebalus* to avoid having two pentatomids in subgroup 2. Subgroup 1 consisted of *Musca*, *Spodoptera* (noctuid caterpillar), *Gryllus* (cricket), *Oebalus* (stinkbug), and *Polygyra* (land snail). Subgroup 2 included *Musca*, *Chauliognathus* (soldier beetle larva), *Euschistus* (stinkbug), *Clubiona* (spider), and *Disonycha* (leaf beetle). These two subgroups were used in 40 initial trials. Ten trials involving each subgroup were run in daylight (20 trials), and the remaining 20 trials were run at night under red light. The latter

Table 1. Percentage biomass-occurrence of the most frequently utilized prey genera in the diet of *Hyla cinerea*.

| Genus | Family | Number | Stomachs with item | Est. biomass (g) | Adj. %BO |
|---|---|---|---|---|---|
| *Spodoptera* (larva) | Noctuidae | 23 | 21 | 2.03 | 20.39 |
| *Chauliognathus* (larva) | Cantharidae | 46 | 32 | 0.79 | 15.73 |
| *Gryllus* | Gryllidae | 6 | 6 | 0.77 | 8.66 |
| *Euschistus* | Pentatomidae | 12 | 11 | 0.43 | 6.76 |
| *Polygyra* | Polygyridae | 8 | 8 | 0.53 | 6.41 |
| *Disonycha* | Chrysomelidae | 22 | 11 | 0.31 | 5.75 |
| *Palthus* | Noctuidae | 12 | 9 | 0.32 | 5.31 |
| *Clubiona* | Clubionidae | 22 | 18 | 0.13 | 4.81 |
| *Oebalus* | Pentatomidae | 9 | 8 | 0.28 | 4.69 |
| *Languria* | Languriidae | 8 | 6 | 0.31 | 4.24 |
| *Cariblatta* | Blattidae | 7 | 6 | 0.20 | 3.40 |
| *Mormidea* | Pentatomidae | 6 | 5 | 0.10 | 2.18 |
| *Ishnoptera* | Blattidae | 2 | 2 | 0.22 | 2.07 |
| *Eudigogus* | Curculionidae | 6 | 5 | 0.08 | 1.99 |
| *Lycosa* | Lycosidae | 4 | 3 | 0.13 | 1.96 |
| *Centrinaspis* | Curculionidae | 11 | 8 | 0.05 | 1.89 |
| *Limonethe* | Ichneumonidae | 3 | 3 | 0.09 | 1.60 |
| *Crematogaster* | Formicidae | 17 | 12 | 0.01 | 1.17 |
| *Pardosa* | Lycosidae | 3 | 2 | 0.03 | 0.99 |

Table 2. Comparison of the percent abundance of prey families represented by at least two individuals in the diet of *Hyla cinerea* with relative abundance estimates derived from tack trap and sweep net sampling. N equals the total number of individuals obtained for each type of sample.

| Family | Stomach | Tack trap | Sweep net | Tack + Sweep |
|---|---|---|---|---|
| Noctuidae | 15.21 | 2.88 | 2.51 | 2.72 |
| Cantharidae | 10.74 | 0.24 | 0.68 | 0.44 |
| Pentatomidae | 8.29 | 0.24 | 5.03 | 2.35 |
| Formicidae | 6.49 | 1.38 | 7.01 | 3.86 |
| Chrysomelidae | 6.04 | 1.56 | 1.37 | 1.48 |
| Curculionidae | 5.82 | 0.60 | 2.44 | 1.41 |
| Clubionidae | 5.15 | 0.78 | 2.06 | 1.34 |
| Alleculidae | 4.70 | 0.06 | 0.08 | 0.07 |
| Sminthuridae | 3.58 | 17.66 | 0.23 | 9.97 |
| Gryllidae | 3.13 | 1.32 | 0.76 | 1.07 |
| Phalangidae | 2.68 | 0.30 | 0.00 | 0.17 |
| Blattidae | 2.24 | 0.00 | 0.23 | 0.10 |
| Cicadellidae | 2.01 | 13.27 | 12.18 | 12.79 |
| Lycosidae | 2.01 | 0.30 | 2.51 | 1.28 |
| Polygyridae | 1.79 | 0.00 | 0.76 | 0.34 |
| Languriidae | 1.79 | 0.00 | 0.00 | 0.00 |
| Reduviidae | 1.79 | 0.00 | 0.91 | 0.40 |
| Chloropidae | 1.57 | 25.05 | 45.70 | 34.15 |
| Araneidae | 1.57 | 1.62 | 4.64 | 2.96 |

Table 2. Continued.

| Family | Stomach | Tack trap | Sweep net | Tack + Sweep |
|---|---|---|---|---|
| Forficulidae | 1.34 | 0.00 | 0.76 | 0.34 |
| Carabidae | 1.34 | 0.54 | 0.23 | 0.40 |
| Scarabaeidae | 1.34 | 0.00 | 0.15 | 0.07 |
| Tetrigidae | 1.34 | 0.36 | 0.30 | 0.34 |
| Entomobryidae | 0.89 | 28.65 | 0.00 | 16.02 |
| Flatidae | 0.89 | 0.00 | 0.00 | 0.00 |
| Porcellionidae | 0.89 | 0.00 | 0.00 | 0.00 |
| Salticidae | 0.89 | 0.30 | 1.29 | 0.74 |
| Tetragnathidae | 0.67 | 0.06 | 0.61 | 0.30 |
| Dictynidae | 0.67 | 0.00 | 0.00 | 0.00 |
| Ichneumonidae | 0.67 | 0.24 | 0.00 | 0.13 |
| Cerambycidae | 0.67 | 0.00 | 0.00 | 0.00 |
| Staphylinidae | 0.45 | 1.80 | 0.15 | 1.07 |
| Lygaeidae | 0.45 | 0.06 | 0.91 | 0.44 |
| Tettigionidae | 0.45 | 0.12 | 6.32 | 2.85 |
| Phloeothripidae | 0.45 | 0.60 | 0.15 | 0.40 |
| N | 447 | 1665 | 1313 | 2978 |

experiments were an attempt to determine if prey selection was affected by time of day. A total of ten prey in equal ratios (2 prey/genus) were available during each run. Twenty frogs were each used in two experimental trials, once with subgroup 1, the other with subgroup 2. The three most preferred prey from each subgroup were used in the final 15 trials; a different frog was used each time. *Musca* and *Spodoptera* were obtained from the United States Department of Agriculture Insect Research Laboratory, Gainesville, Florida. All other prey were collected on Paynes Prairie.

The frogs were tested in a gridded plexiglass chamber (28 × 28 × 28 cm) with white paper covering three walls of the cube; the front and top were left uncovered to permit observation. The white wooden floor of the chamber had a sliding panel containing two small chambers recessed on opposite sides outside of the cube (see Figure 1, Gardner 1964). This allowed introduction of the frog into the feeding chamber. Ten prey (2/genus) were placed into the chamber 5 min prior to the release of the predator. During the 30 min experiment the following were recorded: order of prey capture, estimated distance of prey from frog at recognition, and behavior of prey just prior to capture.

The following electivity equation ($e_i$) was developed to estimate predator preferences. This equation produces an index that varies from 0, indicating that the prey item is completely ignored by the predator, to 1, indicating that the predator specializes only on that prey:

$$e_i = \frac{\sum_{j(i)} \left(\frac{1}{n_{i(j)/N}}\right) \left(\frac{1}{R_j}\right)}{\sum_{j(i)} \frac{1}{n_{i(j)/N}}}, \qquad (2)$$

where $n_{i(j)}$ is the number of individuals of prey species $i$ present just prior to capture of individual $j$ of the species $i$, $N$ is the total number of all individuals of all prey types present just prior to the capture of individual $j$, and $R_j$ is the ordinal rank of individual $j$ captured by the predator.

None of the measures of preference presented in the literature (Ivlev 1961; Rapport and Turner 1970; Chesson 1978; Cock 1978) considers the order of prey capture. These equations were designed for application to open systems in which the predator encounters only one or few prey types at any given time. In such a system, choice is limited either to pursuing or not pursuing prey coming within reach. In my experiments the predator was simultaneously presented with ten prey items of several prey species. Discretion here included the ability to focus on one prey species in the presence of other, potentially distracting, prey species. Ranking allows assignment of higher values to each successive member of a prey type captured within a rank, thus emphasizing the predator's capacity for type-selection as the absolute abundance of the preferred prey type decreases. Therefore, if a series of one prey type was captured in sequence, the same rank ($R_j$) was assigned to all individuals in that set. In other words, if the first three prey items consumed out of ten possible items (3 different species) were the same kind, each of the three would carry a rank of 1, since any of them could have been captured first. In addition to prey rank, the relative abundance of prey types was calculated at each predation. With the closed system utilized, prey replacement is eliminated and rank order of prey capture becomes extremely important. If prey selection were random, a single predation could almost halve the

chance of a second successive predation on the same species, an obvious departure from natural conditions. The value $e_i$ is relative, and like all measures of preference its value for a particular item will be greatly influenced by alternative choices available at the time of selection. Consequently, mean values of $e_i$ were used for comparing the electivity of the various prey species.

An activity index was developed by recording the behavior of each prey several seconds prior to capture. The following activities were ranked 0 through 5 on the basis of increasing levels of activity: 0--motionless, 1--antennae waving, 2--grooming, 3--searching, 4--crawling, and 5--flying. Searching behavior of prey was defined as vertical and/or lateral waving of the anterior third of the body. If a prey was observed performing several behaviors simultaneously, it was given the highest appropriate ranking. This index is the mean rank of all recorded pre-capture and first attempted capture activity for a particular prey genus. Uneaten prey were assigned a 0 in order to avoid bias that results in an increase in index values for genera that characteristically spend long periods of time motionless and thereby escape predation.

An activity budget was developed for each prey genus by recording the time spent on each characteristic behavior during a 2 min time period. Depending upon the number of behavior patterns commonly displayed by a genus, a total of 6 to 12 min were spent on each individual to record all activity. The behavior of ten individuals from each genus was recorded during daylight and an equal number for each genus was recorded at night under red light. This time budget was for isolated prey and differs from the activity index in that the latter involved interacting individuals and included predator disturbance.

The time budget in conjunction with the level of predation recorded for each activity pattern of each genus allowed the determination of the strength of feeding stimulation ($s$) associated with prey behavior. The following index provides an estimation of the stimulus strength (in predations/h) for each behavior pattern exhibited by prey:

$$s = \frac{P_{i(x)}}{t_{i(x)}\ T_i}, \tag{3}$$

where $P_{i(x)}$ is the number of predations and/or attempted captures on prey genus $i$ performing behavior $x$, $t_{i(x)}$ is the proportion of time normally spent performing behavior $x$ by prey genus $i$ in the absence of the predator, and $T_i$ is the total number of hours prey $i$ was exposed to the predator.

Lastly, the difficulty of capture ($I$) for each prey was calculated by dividing the number of misses of prey $i$ by the number of capture attempts recorded for that prey genus.

## Results

Families of prey represented in the sample population by at least two individuals in the stomach contents of *Hyla cinerea* are presented in Table 2. A list of all identified prey is included in Appendix 2. Spearman's rank correlation was used to compare the proportions of prey from stomachs with those of potential prey available in the habitat. Tests performed using prey families with a minimum of five items in stomachs (N = 7) showed that no significant correlation exists between prey eaten by treefrogs and prey available for consumption. However, a

significant correlation was found when all 35 prey families from Table 2 were compared to the proportions of prey obtained from sweep net ($r_s$ = 0.41, $P$ = 0.02) and combined ($r_s$ = 0.34, $P$ = 0.05) samples. Depending on the number of prey families included in the statistical analysis, it is possible to conclude that either the frog was a non-selective feeder or a discriminating forager. Naturally rare prey families were rarely included in the frogs' diet. Therefore, by adding many infrequently utilized prey families to the Spearman rank analysis, the coefficient increasingly approaches significance.

Since no significant difference (ANOVA, $F$ = 0.01, $P$ = 0.91) was found between the $e_i$'s generated by frogs under the two different light regimes, data from light and dark experiments were combined. *Musca* was the most preferred prey item in laboratory experiments (Table 3). *Spodoptera* and *Chauliognathus* larvae ranked respectively second and third in the initial trials, but were reversed in the standings of the final preference experiments. This is not unexpected since both the latter two prey were highly favored in the field by treefrogs. A comparison of initial $e_i$'s with field ranks determined by *%BO* of the eight natural prey genera revealed a significant correlation between these independent indicators of prey preference (Table 4A).

Prey selection significantly correlates with prey activity (Tables 4B and 5) and length (Tables 4C and 6) but not mass (Table 4D). A parametric test for partial correlation between predator selectivity, prey length, and prey activity indicated that 42% ($r$ = 0.65, $P < 0.1$) and 55% ($r$ = 0.74, $P < 0.05$) of the variability observed in $e_i$ are accounted for by prey activity, and prey length, respectively. Substituting mass for the estimate of size, the variation in $e_i$

Table 3. Mean electivity coefficients ($e_i$) for nine prey genera. N equals the number of preference experiments performed. The number of each genus used equals 2N.

| Prey Genus | Initial | | | Final | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | N | $\bar{X}$ | SE | N | $\bar{X}$ | SE | N |
| *Musca* | 0.416 | 0.04 | 40 | 0.408 | 0.06 | 15 | 0.414 | 0.05 | 55 |
| *Spodoptera* | 0.340 | 0.05 | 20 | 0.137 | 0.03 | 15 | 0.253 | 0.05 | 35 |
| *Chauliognathus* | 0.269 | 0.03 | 20 | 0.209 | 0.06 | 15 | 0.243 | 0.05 | 35 |
| *Gryllus* | 0.136 | 0.03 | 20 | 0.131 | 0.03 | 15 | 0.134 | 0.03 | 35 |
| *Euschistus* | 0.075 | 0.04 | 20 | 0.003 | 0.01 | 15 | 0.045 | 0.03 | 35 |
| *Oebalus* | 0.074 | 0.02 | 20 | | | | | | |
| *Disonycha* | 0.071 | 0.02 | 20 | | | | | | |
| *Clubiona* | 0.049 | 0.01 | 20 | | | | | | |
| *Polygyra* | 0.000 | 0.00 | 20 | | | | | | |

Table 4. Spearman's coefficient of rank correlation, $r_s$, for predator-prey variables (two-tailed test). N equals the number of prey genera.

| Correlation | N | $r_s$ | $P$ |
|---|---|---|---|
| A. Prey rank (*%BO*) *vs* electivity | 8 | 0.79 | 0.021 |
| B. Prey rank (*%BO*) *vs* prey activity | 8 | 0.75 | 0.031 |
| C. Prey rank (*%BO*) *vs* prey length (stomach) | 8 | 0.76 | 0.028 |
| D. Prey rank (*%BO*) *vs* prey mass (stomach) | 8 | 0.57 | 0.139 (NS) |
| E. Electivity *vs* prey activity | 9 | 0.83 | 0.006 |
| F. Electivity *vs* prey length | 9 | 0.42 | 0.265 (NS) |
| G. Electivity *vs* prey mass | 9 | 0.00 | 1.000 (NS) |
| H. Electivity *vs* capture difficulty | 9 | -0.37 | 0.332 (NS) |
| I. Electivity *vs* medium cm from frog | 9 | -0.45 | 0.223 (NS) |
| J. Electivity *vs* % prey within 10 cm | 9 | 0.29 | 0.452 (NS) |
| K. Electivity *vs* % prey within 5 cm | 9 | 0.67 | 0.047 |
| L. Prey activity *vs* % prey within 5 cm | 9 | 0.90 | 0.001 |

Table 5. Indicators of relative activity for nine prey genera. The activity index is calculated as the mean rank of all recorded precapture activity as well as activity prior to the first unsuccessful capture attempt. The activity scale runs from 0 to 5, 5 representing the greatest activity level. *I* equals misses/attempts.

| Prey Genus | Index of Prey Activity | | | Capture Difficulty |
|---|---|---|---|---|
| | $\bar{X}$ | SE | N | *I* |
| *Musca* | 3.3 | 0.2 | 110 | 0.47 (68/145) |
| *Spodoptera* | 2.1 | 0.2 | 70 | 0.02 ( 1/ 43) |
| *Chauliognathus* | 2.2 | 0.2 | 70 | 0.23 (10/ 44) |
| *Gryllus* | 2.0 | 0.2 | 70 | 0.49 (28/ 57) |
| *Euschistus* | 1.4 | 0.2 | 70 | 0.85 (23/ 27) |
| *Oebalus* | 1.0 | 0.3 | 40 | 0.20 ( 2/ 10) |
| *Disonycha* | 0.6 | 0.2 | 40 | 0.00 ( 0/ 8) |
| *Clubiona* | 1.7 | 0.3 | 40 | 0.52 (11/ 21) |
| *Polygyra* | 1.0 | 0.3 | 40 | 1.00 (13/ 13) |

Table 6. Size of nine prey genera. Widest shell diameter was used for measurements of *Polygyra*. Measurements of shell width/extended length for five *Polygyra* resulted in the addition of 65% of the shell diameter to the mean shell width for the estimate of extended length shown in parentheses.

| Prey Genus | Live Measurements | | | | | Estimated Measurements (stomach) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mass (mg) | | | Body length (mm) | | Mass (mg) | | | Body length (mm) | |
| | N | $\bar{X}$ | SE | $\bar{X}$ | SE | N | $\bar{X}$ | SE | $\bar{X}$ | SE |
| *Musca* | 10 | 12 | 10 | 6.4 | 0.1 | | | | | |
| *Spodoptera* | 20 | 158 | 10 | 24.9 | 1.0 | 20 | 102 | 30 | 17.0 | 2.0 |
| *Chauliognathus* | 20 | 16 | 10 | 10.6 | 0.5 | 46 | 17 | 10 | 10.8 | 0.6 |
| *Gryllus* | 20 | 244 | 50 | 14.7 | 0.9 | 7 | 149 | 50 | 10.4 | 1.0 |
| *Euschistus* | 20 | 76 | 10 | 12.1 | 0.4 | 12 | 36 | 10 | 9.5 | 0.5 |
| *Oebalus* | 20 | 32 | 10 | 9.7 | 0.2 | 9 | 31 | 10 | 9.6 | 0.3 |
| *Disonycha* | 20 | 18 | 10 | 6.9 | 0.1 | 22 | 14 | 10 | 6.3 | 0.1 |
| *Clubiona* | 20 | 13 | 10 | 6.0 | 0.2 | 18 | 8 | 10 | 4.0 | 0.3 |
| *Polygyra* | 18 | 60 | 10 | 5.8 (9.6) | 0.1 | 7 | 68 | 20 | 5.5 (9.1) | 0.7 |

accounted for by activity and mass is 51% ($r$ = 0.71, $P < 0.05$) and 0.01% ($r$ = 0.009, $P > 0.05$) respectively. When considering all nine prey items including *Musca*, prey selection is significantly associated with prey activity (Table 4E) but not with size (Tables 4F and G). Partial correlations indicated that activity accounts for 77% ($r$ = 0.88, $P < 0.05$) of the variation observed in $e_i$, whereas length accounts for only 21% ($r$ = 0.46, $P > 0.05$) of the observed variation. Using mass as an estimator of size, mass accounts for 0.25% ($r$ = -0.05, $P > 0.05$) of the observed variation of $e_i$, whereas activity accounts for 74% ($r$ = 0.86, $P < 0.05$) of the observed variability of the electivity coefficients.

The activity time budget for each genus is presented in Table 7. There was no significant difference ($t$ tests, $P > 0.05$) in prey behavior between day and night observations, and therefore the data were combined. The activity index may be considered circular, since it relies on predator response as a signal for recording prey behavior. Nevertheless, this index best represents the observed activity of prey during an experiment. The prey-specific activity indices are significantly correlated ($r_s$ = 0.59, $P$ = 0.048, one-tailed test) with activity ranks obtained from time budget data. These ranks were derived by multiplying the numerical value (0-5) of each type of behavior by the proportion of time devoted to that behavior (Table 7). Therefore, the activity index does correlate with the activity time budget, an independent estimator of the mean level of prey activity.

The activity patterns displayed by the prey and the proportion of time devoted by the prey to each behavior influence prey selection. The strength of the feeding stimulus associated with each prey genus

Table 7. Activity time budget and summary of predations associated with each activity pattern of nine prey. Note: *a* = value for palp drumming. *b* = value for spinning silken retreat.

| Genus | Variable | N | Behavior Pattern | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Motion-less | Antennae wave | Groom | Search | Crawl | Fly |
| *Musca* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 8 ± 3 | - | 40 ± 4 | - | 50 ± 4 | 3 ± 0 |
| | 2. # eaten | 77 | - | - | 5 | - | 64 | 8 |
| | 3. # missed behavior noted | 15 | - | - | 2 | - | 12 | 1 |
| | 4. # not eaten | 18 | - | - | - | - | - | - |
| *Spodoptera* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 47 ± 6 | - | 6 ± 2 | 22 ± 3 | 26 ± 5 | - |
| | 2. # eaten | 42 | 1 | - | - | 21 | 20 | - |
| | 3. # missed behavior noted | 1 | - | - | - | - | 1 | - |
| | 4. # not eaten | 27 | - | - | - | - | - | - |
| *Chauliognathus* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 3 ± 3 | - | 5 ± 1 | 12 ± 8 | 79 ± 3 | 0 ± 0 |
| | 2. # eaten | 34 | 1 | - | - | 2 | 31 | - |
| | 3. # missed behavior noted | 6 | - | - | - | 1 | 5 | - |
| | 4. # not eaten | 30 | - | - | - | - | - | - |

Table 7. Continued.

| Genus | Variable | N | Behavior Pattern | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Motion-less | Antennae wave | Groom | Search | Crawl | Fly |
| *Gryllus* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 41 ± 6 | 7 ± 2 | 19 ± 3 | - | 33 ± 5 | - |
| | 2. # eaten | 29 | 1 | 3 | 1 | - | 24 | - |
| | 3. # missed behavior noted | 12 | - | 3 | - | - | 9 | - |
| | 4. # not eaten | 29 | - | - | - | - | - | - |
| *Euschistus* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 31 ± 6 | 4 ± 2 | 23 ± 2 | - | 41 ± 6 | 0 ± 0 |
| | 2. # eaten | 4 | - | 1 | - | - | 3 | - |
| | 3. # missed behavior noted | 21 | - | 1 | 1 | - | 17 | 2 |
| | 4. # not eaten | 45 | - | - | - | - | - | - |
| *Oebalus* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 54 ± 6 | 0 ± 0 | 18 ± 3 | - | 27 ± 6 | 0 ± 0 |
| | 2. # eaten | 8 | - | - | - | - | 8 | - |
| | 3. # missed behavior noted | 2 | - | - | - | - | 2 | - |
| | 4. # not eaten | 30 | - | - | - | - | - | - |

Table 7. Continued.

| Genus | Variable | N | Behavior Pattern | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Motion-less | Antennae wave | Groom | Search | Crawl | Fly |
| *Disonycha* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 31 ± 4 | 6 ± 1 | 40 ± 3 | - | 22 ± 5 | 0 ± 0 |
| | 2. # eaten | 8 | - | 2 | 1 | - | 5 | - |
| | 3. # missed behavior noted | 0 | - | - | - | - | - | - |
| | 4. # not eaten | 32 | - | - | - | - | - | - |
| *Clubiona* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 55 ± 8 | 0 ± 0[a] | 5 ± 2 | 19 ± 7[b] | 21 ± 4 | - |
| | 2. # eaten | 10 | - | - | - | 1 | 9 | - |
| | 3. # missed behavior noted | 7 | - | - | - | - | 7 | - |
| | 4. # not eaten | 23 | - | - | - | - | - | - |
| *Polygyra* | 1. % activity time ($\bar{X}$ ± SE) | 20 | 36 ± 8 | - | - | 24 ± 3 | 40 ± 7 | - |
| | 2. # eaten | 0 | - | - | - | - | - | - |
| | 3. # missed behavior noted | 13 | 2 | - | - | 3 | 8 | - |
| | 4. # not eaten | 27 | - | - | - | - | - | - |

while performing a specific behavior is presented in Table 8. Behavior patterns exhibited within a prey genus vary tremendously in their ability to elicit feeding behavior in *Hyla cinerea*. For example, grooming behavior in the cricket (*Gryllus*) is associated with a level of predation of 0.2 captures/h whereas crawling elicits 2.9 predations/h. In addition, similar behavior patterns of different genera vary in their stimulus strength. To the treefrog, crawling flea beetles (*Disonycha*) represent a feeding stimulus 61% less effective than crawling crickets, which in turn represent a feeding stimulus 27% less effective than crawling spiders (*Clubiona*). Since 3.9 predations/h are associated with spider crawling, it is surprising that *Clubiona* was ranked only eighth in overall preference. This low rank is due to the proportion of time the spider remained motionless (54%), greater than any of the other prey included in this experiment. *Musca*'s high rank is due to the combination of two powerful frog orienting stimuli, flight and crawling. The flight-crawl behavioral sequence accounts for 53% of the fly's activity time budget and resulted in 8.1 predations/h. Linkage between searching and crawling behavior patterns, associated with 2.7 and 2.3 predations/h respectively, probably accounts for the high ranking received by *Spodoptera*. Conversely, *Chauliognathus* crawling at 1.3 captures/h is a mildly effective stimulus for a highly ranked prey type, but the soldier beetle larvae spent 80% of their observed time performing this behavior. The combination of crawling and searching behavior (0.7 captures/h) accounts for 92% of the beetle larvae's activity time budget.

Finally, prey selection is not affected by the difficulty involved in capturing a prey (Tables 4H and 5), or the distance of prey

Table 8. Strength of feeding stimulus ($s$) associated with prey behavior. Values in the table are for $s$ = captures/h (see text). $a$ = values for palp drumming. $b$ = value for spinning silken retreat.

| Prey Genus | Behavior | | | | | |
|---|---|---|---|---|---|---|
| | Motionless | Antennae wave | Groom | Search | Crawl | Fly |
| *Musca* | 0.0 | - | 0.3 | - | 2.8 | 5.3 |
| *Spodoptera* | 0.1 | - | 0.0 | 2.7 | 2.3 | - |
| *Chauliognathus* | 0.9 | - | 0.0 | 0.7 | 1.3 | - |
| *Gryllus* | 0.1 | 2.6 | 0.2 | - | 2.9 | - |
| *Euschistus* | 0.0 | 1.4 | 0.1 | - | 1.4 | 2/0 |
| *Oebalus* | 0.0 | 0.0 | 0.0 | - | 1.9 | 0.0 |
| *Disonycha* | 0.0 | 1.6 | 0.1 | - | 1.1 | - |
| *Clubiona* | 0.0 | 0.0[a] | 0.0 | 0.3[b] | 3.9 | - |
| *Polygyra* | 0.3 | - | - | 0.6 | 1.0 | - |

Table 9. Percentage of predation experienced by each genus within a specified distance from the treefrog. Included are estimated median distances of frogs from prey just prior to pursuit and capture.

| Prey Genus | Distance from Predator | | | |
|---|---|---|---|---|
| | N | 0-5 cm | 0-10 cm | Median (cm) |
| *Musca* | 84 | 71 | 92 | 4.0 |
| *Spodoptera* | 39 | 46 | 72 | 7.5 |
| *Chauliognathus* | 37 | 62 | 76 | 5.0 |
| *Gryllus* | 36 | 44 | 50 | 10.3 |
| *Euschistus* | 22 | 41 | 46 | 11.5 |
| *Oebalus* | 16 | 38 | 50 | 10.3 |
| *Disonycha* | 8 | 38 | 63 | 8.0 |
| *Clubiona* | 8 | 44 | 50 | 10.3 |
| *Polygyra* | 9 | 44 | 78 | 7.5 |

from the predator prior to attack (Tables 4I, J and 9). However, there is a significant association between $e_i$ and the percentage of predations occurring within a 0 to 5 cm distance from the frog (Table 4K). In turn, the percentage of predations between 0 and 5 cm is highly correlated with prey activity, emphasizing the greater probability of predator encounter associated with more active prey (Table 4L).

## Discussion

*Spodoptera* and *Chauliognathus* were the two prey items most frequently consumed by *Hyla cinerea* in the field. Both are worm-like, a configuration shown to be a strong stimulus in eliciting feeding (Ewert 1974; Ingle 1976). However, *Musca* was the most consistently preferred food item offered in laboratory experiments in which prey were equally available at the begining of each trial. Previous work (Freed 1980*b*) showed that *Musca* was most preferred, although the mean $e_i$ generated from that study was 0.745 versus the present $e_i$ of 0.416. Electivity is relative, and can be greatly influenced by the alternative choices available at the time of selection. The lower $e_i$ for *Musca* in this study reflects the greater stimulus value of alternative prey. Mosquitoes were the only alternate prey available in the previous study; they are almost completely ignored by treefrogs in their natural habitat.

*Hyla cinerea* is capable of consistently selecting specific prey. This high degree of discrimination is emphasized by similar ranks generated in laboratory preference experiments and ranks based on stomach content analysis of the sample population. Three prey-specific variables influence selection under laboratory conditions: prey size,

prey activity, and the frequency of occurrence of various attack-inducing behaviors. Prey mass, unlike length, may not be easily discernible at a distance, and is not an important parameter. Prey length does influence prey selection in the field. However, this association does not exist in laboratory experiments that include house flies. This indicates that even though prey length is an important cue utilized by the frog, it could be overshadowed by the cues provided by prey activity. *Hyla cinerea* differentially selects prey in relation to the proportion of time a prey species remains active, as well as the types of activity most often displayed. An increase in the proportion of a specific prey activity results in a subsequent increase in the functional density of that prey (Werner and Hall 1974), thus resulting in greater predation. Since the various behavior patterns within a prey genus are not equally stimulating to frogs, the stimulus value of prey is not fixed, but (in accordance with its activity time budget) will fluctuate over time. Similar behaviors shared among different prey also vary in their ability to elicit feeding in *H. cinerea*. This variation is most likely related to genus-specific differences in configuration, and in the case of crawling and flight, differences in velocity (Luthardt and Roth 1979*a*). *Hyla cinerea* select prey that most frequently display the behaviors of greatest stimulus value. Thus if *Clubiona* partitioned their activity time in a manner similar to *Musca* or *Chauliognathus*, these spiders would probably rank equal to or higher than house flies or soldier beetles in the diet of the treefrog.

The difficulty involved in capturing each prey does not influence prey choice; however, several interesting observations were noted. First, the humeral spines located on the prothorax of *Euschistus* are an

effective predator deterrent. Treefrogs repeatedly rejected stinkbugs after lodging these spines between their jaws. Second is the unexpected difficulty encountered by frogs attempting to capture the pulmonate land snail *Polygyra*. The adhesion of the snail to the substratum by mucus secretion interrupted the timing of the frog. This resulted in the jaws closing slightly before the snail was completely in the mouth, forcing the snail off the frog's tongue. Finally, *Chauliognathus* larvae, assumed to be distasteful due to the presence of cantharidin (Carrel and Eisner 1974), were consistently eaten by some individuals and completely ignored by others. The propensity of some individuals to select *Chauliognathus* could be attributed to learning (Luthardt and Roth 1979*b*) or possibly to polymorphism (Arnold 1977) in the hylid population.

In conclusion, the great variety of behavior patterns exhibited by the different prey form a complex of cues that differentially influence feeding behavior in *Hyla cinerea*. Behavioral patterns vary within and among prey genera in quality, *i.e.*, in the ability to elicit orientation and prey capture by the frog. Selection is closely related to the time devoted by each prey to specific behaviors. Size, as measured by length, is also a cue used in the selection of prey but can be overshadowed by prey behavior. Behavior modification is probably a major evolutionary process affecting the interactions between visually-oriented predators and their prey. Predators that utilize only cues that represent large proportions of the prey's activity time budget should have a selective advantage. Conversely, a reallocation of the prey's available activity time away from high risk behavior patterns or changes in the level of activity thus altering its stimulus value are

mechanisms that may function over ontogenetic as well as evolutionary time.

SECTION II

VISUAL CUES: YOU LOOK GOOD ENOUGH TO EAT

## Introduction

Discrimination is a prerequisite for prey selection. Upon encountering potential prey, predators evaluate the suitability of that item. This evaluation results in the decision to pursue or ignore the prey. Behavioral studies of different species of anurans demonstrated that size (Ewert 1968, 1970; Ingle 1968, 1971; Ingle and Cook 1977), configuration (Borchers *et al.*, 1978; Ewert and Kehl 1978; Ewert *et al.*, 1979; Ingle and McKinley 1978), velocity (Ewert 1968, 1970; Ewert *et al.*, 1979) and movement pattern (Borchers *et al.*, 1978; Ingle 1975) of artificial prey stimuli are important parameters in eliciting feeding behavior. Since no biological relationship exists between the natural food items and the dummy prey stimuli used, data that are the product of predator encounters with artificial prey lack ecological significance.

In Section I, I showed that green treefrogs (*Hyla cinerea*) select natural prey according to the behavior patterns displayed by the prey, and the proportion of time devoted to each prey-specific behavior (also see Freed 1980*b*). Prey length was also an important selection parameter, but its value as a cue may be overshadowed by prey activity. The following hypotheses were formed based on experimental observations: (a) preferred prey items elicit larger turns during orientation by *H. cinerea* than prey items of lower preference, (b) the time involved

for the predator to recognize and attack prey, as well as the latency period separating these two events, varies inversely with prey rank in the frog's diet, and (c) highly preferred prey elicit predator recognition at greater distances than lower ranked prey. The purposes of this study were (1) to test these hypotheses and determine if these variables are suitable indicators of predator preference, and (2) to quantify the natural cues utilized by the green treefrog during the process of prey selection.

## Methods

Ten adult (6 males, 4 females) *Hyla cinerea* (SVL: $\overline{X} \pm SE = 4.6 \pm 0.1$ cm, Range: 3.8 - 4.9 cm) were collected in Gainesville, Florida. Treefrogs were maintained in 1 L containers, each housing three or four frogs. Upon capture, individuals were fed once with house flies. Frogs were then starved four days prior to and between experimental trials to minimize any effect of satiation. The frogs were fed only during the experimental trials. The experimental chamber was the plexiglass cube described previously. The top and the front plexiglass walls were left uncovered to allow lighting and filming of the predator-prey encounter. A digital stopwatch was positioned in the lower left corner of the chamber allowing timing of sequences.

Previous experiments in Section I allowed treefrogs to choose from a variety of prey; the present study focused on one-on-one predator-prey encounters. The same nine invertebrates (Table 3) described in Section I were used in these trials. Frogs were placed in the experimental chamber a minimum of 15 min prior to the beginning of the experimental trial. After a frog assumed a resting position, a prey item was placed

in the chamber at the farthest point away from and directly behind the frog. An aspirator was used to position the prey item. At the time the prey was placed in the chamber, the stopwatch and the movie camera were started simultaneously. Since the fly was known to be a highly preferred food item, it was always used to start a session, testing the readiness of the frog. After capturing the prey, the next trial did not begin until the frog reassumed a resting position. If a prey was ignored by the treefrog, the trial was terminated at the end of 5 min.

Predator-prey interactions were recorded on 16 mm Kodak black and white Tri-X reversal film using a motorized Bolex H-16 Rex movie camera with a 10 mm wide angle lens. A remote controlled Viewlex M-16 TA 16 mm stop-frame projector allowed single frame analysis of predator and prey. The following data were recorded directly from the film: time to recognition of prey, time to attack, prey behavior at the time of recognition, prey behavior just prior to prey capture, prey length, prey velocity, and coordinate location of frog and prey at the time of prey recognition by the predator. Recognition was defined as the first visible movement of the frog in response to the prey. This movement varied from a head twitch to the initiation of orientation towards the prey item. Since prey width could not always be measured accurately from the film, it was estimated from measurements of prey length using various length-width regression equations developed for each prey (Appendix 3). The period of latency separating recognition and attack was calculated as the difference between these variables.

Location data were used to recreate the positions of predator and prey at the time of prey recognition by the frog. This was done by using a gridded cardboard box that was identical in size to the feeding

chamber. Two walls were removeable to facilitate measurements: a model frog and prey were attached to the walls in their respective positions, and a string was tightly strung from the prey to a point between the model frog's eyes. Three dimensional orientation (Mardia 1972) by the treefrog was determined by measuring the angle of rotation about the horizontal axis of the frog and the frog's angle of vertical elevation towards the prey. The distance between the predator and the prey item was also measured. The angle of the frog's visual field subtended by prey ($\theta$) was calculated by incorporating the size of the prey (length and width) and the distance at the time of recognition:

$$\theta = \text{TANGENT}^{-1}\left(\frac{\text{SIZE}}{\text{DISTANCE}}\right). \quad (4)$$

Since Ingle and Cook (1977) showed that within 15 cm, *Rana pipiens* feeding behavior is dependent on real object size and visual angles are only utilized at farther distances, visual angles are presented only for prey that were recognized by the frog at distances greater than 15 cm.

## Results

The mean spherical direction in which *Hyla cinerea* oriented toward each prey is presented in Figure 1 and Table 10. A Watson and Williams multi-sample test (Mardia 1972) indicated that a significant difference exists ($F = 2.18$; df = 8, 100; $P < 0.05$) among the mean angles rotated by treefrogs toward the various prey types. However, Spearman's test for rank correlation showed that no significant correlation exists between prey ranks ($e_i$) generated in laboratory preference experiments (Table 3) and the frog's mean directional rotation towards a prey genus (Table 11A).

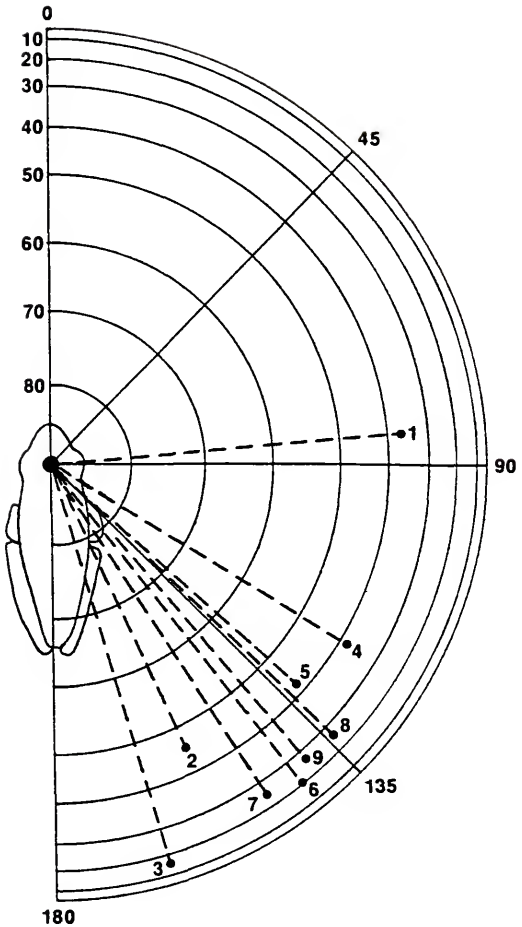


Figure 1. Schematic illustration showing mean rotational orientation towards each of nine prey. The frog is located at the center of the sphere and the prey, represented by dots, are located on the surface of the sphere. Numbers 1 through 9 refer to prey listed in Table 10. Concentric circles represent degrees latitude that define vertical location of prey.

Table 10. Mean spherical direction (Mardia 1972) of the orientation of *Hyla cinerea* towards various prey genera. S = the spherical variance. N = the number of predator-prey encounters analyzed.

| | Prey Genus | Horizontal Angle (degrees) | Vertical Angle (degrees) | S | N |
|---|---|---|---|---|---|
| 1. | *Musca* | 86 | 37 | 0.3 | 18 |
| 2. | *Spodoptera* | 155 | 45 | 0.2 | 16 |
| 3. | *Chauliognathus* | 164 | 16 | 0.1 | 9 |
| 4. | *Gryllus* | 122 | 39 | 0.2 | 14 |
| 5. | *Euschistus* | 132 | 42 | 0.3 | 13 |
| 6. | *Oebalus* | 142 | 20 | 0.1 | 10 |
| 7. | *Disonycha* | 147 | 25 | 0.1 | 8 |
| 8. | *Clubiona* | 134 | 26 | 0.2 | 9 |
| 9. | *Polygyra* | 140 | 26 | 0.1 | 12 |

The average time used to identify and subsequently attack each prey, the latency period separating these two events, and the mean distance of the prey from the predator at the time of recognition are presented in Table 12. A Kruskal-Wallis one-way analysis of variance (Siegel 1956) indicated that time between prey introduction and recognition by the frog does not significantly differ among the nine prey ($\chi^2$ = 13.6, df = 8, $P$ = 0.09). No significant correlation exists between predator electivity ($e_i$) and the frog's time to recognition of prey (Table 11B). However, when considering only the eight natural prey, a significant negative correlation was found between the time to predator recognition and the average crawling velocity of the prey (Table 11C). The correlation for all prey, including the house fly, is also negative but not significant (Table 11C). A significant difference did exist among the treefrog's latency periods separating the times for recognition and attack ($\chi^2$ = 31.5, df = 8, $P$ = 0.0001). However, no association was found between predator electivity and these latency periods (Table 11D). Similarly, there are significant differences in the amount of time preceding predator attack ($\chi^2$ = 25.7, df = 8, $P$ = 0.001), but there is no significant correlation between $e_i$ and the time to attack for each prey genus (Table 11E). In addition, the average distance at the time of recognition for each prey does not significantly differ ($\chi^2$ = 9.9, df = 8, $P$ = 0.27), and no significant correlation is observed when rank order of prey selection is compared to these distances (Table 11F).

Significant differences exist for both length ($\chi^2$ = 81.6, df = 8, $P$ = 0.0001) and width ($\chi^2$ = 80.6, df = 8, $P$ = 0.0001) among the nine prey genera (Table 13). A significant correlation with prey selection

Table 11. Spearman's coefficient of rank correlation, $r_s$, for predator-prey variables from one-on-one encounters of *Hyla cinerea* with prey (two-tailed test).

| Correlation | Natural Prey (N = 8) | | Prey (N = 9) | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| A. Electivity *vs* horizontal angle of orientation | 0.33 | 0.420(NS) | -0.07 | 0.865(NS) |
| B. Electivity *vs* time to predator recognition | -0.14 | 0.736(NS) | 0.05 | 0.898(NS) |
| C. Time to predator recognition *vs* prey velocity | -0.74 | 0.037 | -0.55 | 0.125(NS) |
| D. Electivity *vs* predator latency to attack | -0.14 | 0.736(NS) | -0.20 | 0.606(NS) |
| E. Electivity *vs* time to attack | 0.02 | 0.955(NS) | 0.17 | 0.668(NS) |
| F. Electivity *vs* prey distance at recognition | 0.40 | 0.320(NS) | -0.02 | 0.966(NS) |
| G. Electivity *vs* prey length | 0.83 | 0.010 | 0.33 | 0.379(NS) |
| H. Electivity *vs* prey width | -0.33 | 0.420(NS) | -0.50 | 0.171(NS) |
| I. Electivity *vs* length/width ratio of prey | 0.67 | 0.071(NS) | 0.55 | 0.125(NS) |
| J. Electivity *vs* visual angle of prey length at distances $\geq$ 15 cm | 0.76 | 0.028 | 0.23 | 0.546(NS) |

Table 11. Continued.

| Correlation | Natural Prey (N = 8) | | Prey (N = 9) | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| K. Electivity *vs* visual angle of prey width at distances $\geq$ 15 cm | -0.41 | 0.320(NS) | -0.43 | 0.244(NS) |
| L. Electivity *vs* prey velocity (crawling) | 0.17 | 0.693(NS) | 0.37 | 0.332(NS) |
| M. Stimulus of crawling prey *vs* predator latency | -0.69 | 0.058(NS) | -0.70 | 0.036 |
| N. Stimulus of crawling prey *vs* prey velocity | 0.67 | 0.071(NS) | 0.73 | 0.025 |
| O. Electivity *vs* stimulus of crawling prey | 0.29 | 0.493(NS) | 0.33 | 0.381(NS) |

Table 12. Response times of *Hyla cinerea* for nine prey genera. Distance was recorded at the time of prey recognition.

| Prey Genus | | Time to Recognition (sec) | Latency (sec) | Time to Attack (sec) | Distance (cm) | N |
|---|---|---|---|---|---|---|
| *Musca* | $\bar{X}$ | 70.8 | 12.5 | 86.4 | 18.0 | 16 |
| | SE | 23.8 | 4.8 | 25.7 | 3.3 | |
| *Spodoptera* | $\bar{X}$ | 71.1 | 20.5 | 91.6 | 27.4 | 15 |
| | SE | 22.3 | 4.2 | 23.0 | 1.4 | |
| *Chauliognathus* | $\bar{X}$ | 46.5 | 14.6 | 61.1 | 22.1 | 9 |
| | SE | 22.5 | 7.9 | 29.6 | 3.1 | |
| *Gryllus* | $\bar{X}$ | 25.8 | 19.8 | 52.2 | 28.2 | 12 |
| | SE | 10.3 | 5.4 | 16.3 | 3.5 | |
| *Euschistus* | $\bar{X}$ | 40.9 | 45.1 | 70.9 | 19.6 | 13 |
| | SE | 22.4 | 37.3 | 42.2 | 2.8 | |
| *Oebalus* | $\bar{X}$ | 17.1 | 8.9 | 22.7 | 21.1 | 10 |
| | SE | 4.0 | 2.2 | 3.3 | 2.6 | |
| *Disonycha* | $\bar{X}$ | 47.6 | 23.2 | 70.8 | 21.0 | 8 |
| | SE | 29.9 | 17.2 | 46.4 | 5.6 | |
| *Clubiona* | $\bar{X}$ | 41.3 | 4.6 | 45.8 | 20.9 | 9 |
| | SE | 23.0 | 1.2 | 23.0 | 3.0 | |
| *Polygyra* | $\bar{X}$ | 104.3 | 67.4 | 210.3 | 24.7 | 12 |
| | SE | 29.4 | 20.3 | 39.6 | 2.0 | |

exists for length of natural prey but not when *Musca* is included in the analysis (Table 11G). This indicates that other cues (*e.g.*, activity level and behavior) may be more important during selection than prey size. When prey width was substituted as the variable describing prey size, no significant correlation with $e_i$ was found (Table 11H). However, length/width ratios approach a significant correlation with selection of natural prey (Table 11I).

The mean visual angles subtended by each prey at distances greater than 15 cm from the frog's eye (Table 13) are significantly different for both prey length ($\chi^2$ = 45.4, df = 8, $P$ = 0.0001) and prey width ($\chi^2$ = 54.3, df = 8, $P$ = 0.0001). The mean angles subtended in the visual field of the frog by the lengths of the eight natural prey are significantly correlated with prey selection (Table 11J). Including the house fly in this comparison eliminates this association (Table 11J). Again, the activity level and behavior that characterize *Musca* may have compensated for the fly's small visual angle and induced the frog to select it over prey subtending larger angles. Likewise, no correlation was found relating prey selection to the visual angles subtended by the width of prey as perceived by the frog (Table 11K).

Even though significant differences exist among the crawling velocities of the nine prey types ($\chi^2$ = 58.8, df = 8, $P$ = 0.0001), no significant association was found that relates these velocities to the selection of invertebrate food items by *Hyla cinerea* (Table 11L). The stimulus value of crawling in the eight natural prey approaches a significant negative correlation with the latency period separating predator recognition and attack (Table 11M). This negative association is significant when all nine prey items are considered (Table 11M).

Table 13. Prey cues possibly utilized by *Hyla cinerea* during the process of prey selection.

| Prey Genus | | Size Length (mm) | Size Width (mm) | Visual Angle Length ≥ 15 cm (degrees) | Visual Angle Length ≥ 15 cm (degrees) | Crawling Velocity (cm/sec) |
|---|---|---|---|---|---|---|
| *Musca* | $\bar{X}$ | 6.3 | 2.1 | 1.5 | 0.5 | 4.9 |
| | SE | 0.1 | 0.1 | 0.2 | 0.1 | 0.6 |
| | N | 16 | 16 | 11 | 11 | 14 |
| *Spodoptera* | $\bar{X}$ | 20.9 | 2.8 | 4.6 | 0.6 | 0.3 |
| | SE | 1.0 | 0.2 | 0.3 | 0.0 | 0.1 |
| | N | 14 | 14 | 14 | 14 | 7 |
| *Chauliognathus* | $\bar{X}$ | 9.6 | 1.9 | 2.2 | 0.4 | 1.4 |
| | SE | 0.7 | 0.1 | 0.2 | 0.1 | 0.1 |
| | N | 9 | 9 | 7 | 7 | 10 |
| *Gryllus* | $\bar{X}$ | 12.9 | 3.7 | 2.4 | 0.7 | 5.9 |
| | SE | 1.0 | 0.3 | 0.3 | 0.1 | 1.1 |
| | N | 12 | 12 | 10 | 10 | 10 |
| *Euschistus* | $\bar{X}$ | 11.9 | 8.3 | 2.6 | 1.8 | 1.6 |
| | SE | 0.5 | 0.4 | 0.3 | 0.2 | 0.2 |
| | N | 10 | 10 | 7 | 7 | 12 |
| *Oebalus* | $\bar{X}$ | 9.3 | 4.5 | 2.3 | 1.1 | 1.3 |
| | SE | 0.3 | 0.1 | 0.3 | 0.1 | 0.2 |
| | N | 10 | 10 | 7 | 7 | 6 |

Table 13. Continued.

| Prey Genus | | Size Length (mm) | Size Width (mm) | Visual Angle Length ≥ 15 cm (degrees) | Visual Angle Length ≥ 15 cm (degrees) | Crawling Velocity (cm/sec) |
|---|---|---|---|---|---|---|
| *Disonycha* | $\bar{X}$ | 6.3 | 3.0 | 1.6 | 0.8 | 0.9 |
| | SE | 0.2 | 0.1 | 0.3 | 0.2 | 0.2 |
| | N | 7 | 7 | 5 | 5 | 6 |
| *Clubiona* | $\bar{X}$ | 6.9 | 2.2 | 1.5 | 0.5 | 4.9 |
| | SE | 0.6 | 0.2 | 0.2 | 0.0 | 0.5 |
| | N | 9 | 9 | 6 | 6 | 9 |
| *Polygyra* | $\bar{X}$ | 7.9 | 5.2 | 1.9 | 1.3 | 0.1 |
| | SE | 0.6 | 0.4 | 0.2 | 0.1 | 0.0 |
| | N | 12 | 12 | 12 | 12 | 4 |

The stimulus value of crawling prey is positively correlated with the characteristic crawling velocity of that prey (Table 11N). However, the stimulus value of crawling prey is not significantly associated with prey selection (Table 11O).

## Discussion

Prey/non-prey discrimination at the level of the retina and the optic tectum of the brain in anurans precedes the behavioral motor response (Schürg-Pfeiffer and Ewert 1981). Toads and frogs express initial interest for a prey item by orienting towards the location of a stimulus (Ewert and Burghagen 1979). My results showed that orienting movements directed towards the stimulus location are not useful indicators of the stimulus value of natural prey in *Hyla cinerea*. *Spodoptera* and *Chauliognathus* larvae are highly preferred by *H. cinerea* both in the laboratory and the field (Table 4). The time utilized in the recognition-attack sequences for these insects does not distinguish these prey from less preferred items. However, prey with high crawling stimulus values do tend to shorten the period of latency separating recognition from attack. Since the configurational meaning of an artificial stimulus is independent of distance in *Alytes obstetricans* and *Bufo bufo*, and the discrimination ability has common components in *A. obstetricans*, *B. bufo*, *Bombina variegata*, *Hyla arboria*, and *H. cinerea* (Ewert and Burghagen 1979), it is surprising to find that *H. cinerea* does not recognize and pursue preferred prey at greater distances than for prey of lower rank. The desirability of the prey item apparently does not influence the degree or alacrity of the response exhibited by the treefrog, but only the probability of the occurrence of that

response. Similarly, Heatwole and Heatwole (1968) found that the motivational state of *Bufo fowleri* (*i.e.*, degree of satiation) does not affect the speed with which responses are given when they occur, but rather whether they occur at all.

Ingle (1968) showed that *Rana pipiens* respond to stimuli on the basis of real object size. Ewert and Burghagen (1979) found that worm-like objects 6 to 12 mm long were particularly attractive to *Hyla cinerea*. Optimal prey catching response occurred when 8 mm long black rectangles were moved at a constant velocity of 20°/s (1 cm/s). This size range approximates the data generated in this study using invertebrate prey whose mean was 10.2 mm (SE = 1.5, N = 9). However, the average length of the most preferred natural prey item (*Spodoptera*) was approximately 21 mm, which is 2.6 times larger than the optimal artificial stimulus cited above.

Prey width alone is not an important selection parameter. However, there is an indication that wild treefrogs select prey that possess length/width ratios greater than 3:1. *Bufo bufo* discriminates between prey and non-prey when dummy stimuli with length/width ratios greater than 3:1 are presented (Ewert 1968; Ewert *et al.*, 1979). Ewert (1976) stated that square objects represent neutral or indifferent stimuli and fall between horizontally (*i.e.*, prey) and vertically (*i.e.*, enemy) oriented rectangles in ability to elicit prey catching behavior in toads. Even so, prey items that are almost "square" (*e.g.*, *Euschistus*) are frequently eaten by treefrogs.

Actual prey size is utilized by frogs within predator-prey distances of 15 cm. Beyond this distance the visual angle cue is involved in prey choice (Ingle 1968, Ingle and Cook 1977). Preferred

stimulus angles at various distances have been reported for a variety of amphibians (Ewert 1968, 1970; Ewert *et al.*, 1979; Himstedt 1967; Ingle 1968, 1971; Ingle and Cook 1977; Roth 1976). Mean visual angles utilized by *Hyla cinerea* varied from 1.5° to 4.6°. The average for all prey genera utilized was 2.3° (SE = 0.3, N = 9) at an average distance of 22.5 cm (SE = 1.2, N = 9). This value is identical to that recorded by Ingle and Cook (1977) for *Rana pipiens*. The functional stimulus angles utilized by *H. cinerea* varied from a minimum of 0.8° for *Disonycha* at 42.5 cm, to a maximum of 6.1° recorded for *Spodoptera* at 20 cm. If frogs did cue on visual angles of prey less than 15 cm distant, the maximum angle utilized was 54.5° for *Musca* at 0.5 cm.

Although *Hyla cinerea* does not always select prey items that characteristically display high crawling velocities, the time to recognition of natural prey is shorter for fast moving invertebrates. Fast crawling prey also possess high stimulus values for treefrogs. Increasing stimulus angular velocity in a range from 5°/s to 40°/s (0.7 cm/s to 4.9 cm/s at 7 cm) increased the overall prey-catching activity of toads towards artificial prey objects (Ewert *et al.*, 1979). Roth (1978) found that the efficacy of a stimulus in eliciting feeding activity in salamanders increases with greater velocity from 0.5 cm/s to 3.1 cm/s. Roth (1976) noted that anurans, unlike the salamander *Hydromantes italicus*, do not show sensitivity to fast movement. *Hydromantes italicus* optimally responds to angular velocities of 4.8°/s to 72°/s and a maximum velocity of 172°/s (6 cm/s) at a distance of 2 cm. The response of *Bufo bufo* decreases significantly at 90°/s (11 cm/s at 7 cm) when compared to its optimal response for stimuli moving at 20°/s (2.4 cm/s) (Ewert *et al.*, 1979). In addition, neurophysiological

studies on *Rana esculenta* showed that responses of class-2-ganglion cells ("bug detectors") decrease sharply when stimulus velocity exceeds 100°/s and almost cease at 140°/s (Finkelstein and Grüsser 1965). However, treefrogs do orient toward flying *Musca*. Flies have an average flight velocity of 93.8 cm/s (SE = 6.18, N = 3). The estimated angular velocity for a fly in flight 18 cm (Table 12) away from the frog exceeds 300°/s. *Musca* commonly walks within 2 cm of resting treefrogs. Average crawling speed at this distance approximately equals an angular velocity of 140°/s; this corresponds to the point at which class-2-ganglion cease responding in *Rana esculenta*.

In addition to prey size and velocity, activity patterns displayed by prey are also important parameters in eliciting feeding response in amphibians. Small squares, known to be poor stimuli for eliciting prey capture in *Bufo bufo*, are more attractive if moved in a step-wise manner rather than in a continuous fashion (Borchers *et al.*, 1978). Ingle (1975) noted that discontinuous motion facilitates prey capture in *Rana*. In *Hydromantes*, step-wise movement is more effective than continuous moving stimuli for eliciting fixation and approach (Roth 1976, 1978). Luthardt and Roth (1979*a*) stated that stimuli of certain orientation must move in a specific manner and at specific velocities in order to elicit optimal prey catching behavior in *Salamandra salamandra*. Prey selection by *Hyla cinerea* is influenced by the activity patterns exhibited by the prey and the proportion of the time each prey genus devotes to each behavior pattern (Section 1, p. 19). Analysis indicated that 62% of all prey were crawling at the time of recognition and 67% were performing the same behavior just prior to predation. Even so, treefrog preference is not associated with the stimulus value of crawling prey, since these

values are time-specific for each prey genus. If each prey spent equal time crawling, the stimulus value for each prey genus would reflect the rank of that prey in the diet of the green treefrog.

The effect of activity patterns on prey selection is best illustrated by *Musca domestica*. Though its configuration provides a poorer stimulus than many of the more elongate natural prey, it was the most often eaten in laboratory experiments. This is due to the fly's characteristic crawling pattern and the linkage of this behavior with flight (Section 1, p. 19). The combination of these two behaviors produces a very discontinuous or jerky activity pattern (see Ingle 1975 and Roth 1978) and accounts for a large proportion of the fly's activity time budget (Table 7).

In conclusion, preference is expressed as the greater probability that orientation and attempted prey capture will occur, not the degree or speed at which these processes take place. The cues utilized by *Hyla cinerea* during the selection of natural prey are prey size, configuration, and activity pattern (which includes the variable prey velocity). This is in close agreement with the findings of experiments using artificial prey stimuli, though *H. cinerea* uses a broader range of some of these parameters with natural prey items. Although the experiments with artificial stimuli are useful in defining cues utilized by frogs during the prey selection process, natural prey elicit responses not predicted from the analysis of anuran encounters with prey dummies.

## CRITIQUE: IF I COULD ONLY DO IT OVER AGAIN

This work possesses certain methodological flaws that are inherent in behavioral studies. A major departure from reality exists since prey activity time budgets lack time periods for foraging behavior. The difficulty of providing food for the various prey and the subsequent decrease in prey visibility (*e.g.*, prey hidden by food) precluded the placing of food in the experimental chamber during time budget analysis. Ideally, time budgets should be developed in the field; however, locating and observing invertebrates in dense vegetation at night is a formidable task. The omission of foraging time from prey activity budgets may be of insignificant consequence since these time budgets were complete for the artificial environment in which the preference testing took place. Conversely, the time prey spend feeding may affect the probability of capture in the field; however, the agreement found between field and laboratory determinations of prey diet rank indicated that this is not the case. A possible explanation for this is that feeding behavior time may already be included in one of the recorded time budget periods. For example, prey may characteristically remain motionless while eating (*e.g.*, *Euschistus* and *Oebalus*) making periods of rest and feeding indistinguishable. The time spent foraging by predatory prey (*e.g.*, *Chauliognathus* and *Clubiona*) is included in the search period; however, the time spent motionless may be underestimated since actual feeding time could add to this period.

Another bias is found in the closed system in which treefrogs were forced to forage. One could argue that prey should be replaced after being eaten, thus maintaining a constant relative prey abundance for predators to choose from. However, natural habitats presumably are not characterized by a constant relative abundance of prey. In addition the electivity equation was specifically designed to analyze prey capture in a closed system. By differentially weighting the order of prey captured in the ranking process, the electivity equation assigns the highest electivity values to prey types that are captured both early and consecutively. Prey that are captured late in the experiment and/or non-consecutively will have low ranks due to the increasing probability of being eaten as total prey abundance decreases.

Finally, the identification of prey taxa may not be important in the foraging ecology of treefrogs. Prey items could be classified as to the presence of important physical and behavioral components utilized by predators during the selection process. Prey with similar morphology, behavior patterns, and size may be classified by the predator as one prey type. Many insects that look and move similarly belong, not only to different genera, but to different orders (*e.g.*, *Spodoptera* and *Chauliognathus* larvae) and, depending on the predator's discriminative ability, may be regarded as one prey (ranked 2,3 in the initial trials and 3,2 in the finals, respectively). In addition, the fifth and sixth ranked prey in this experiment may also be considered a single prey type; though belonging to different genera (*Euschistus* and *Oebalus*) they belong to the same family and exhibit many similar morphological and behavioral features. I assumed that I was offering treefrogs a choice among nine different prey genera, but in reality, frogs may have

recognized only seven distinct types of prey. I consider this and the above criticisms valid, but of minor consequences; they do not alter the conclusions concerning the discriminative ability of *Hyla cinerea* or the visual cues used during the selection process.

APPENDIX 1
PARAMETER ESTIMATES FOR LENGTH-MASS EQUATIONS

Power function model: $y = bx^m$. Length is in mm, mass in mg. *Polygyra* size range is for shell diameter, not extended length.

| Genus | Size Range (mm) | $b$ ($b \times 10^{-2}$) | $m$ | $r$ | N |
|---|---|---|---|---|---|
| *Spodoptera* (larva) | 5.5-33.5 | 2.1 | 2.8289 | 0.99 | 35 |
| *Chauliognathus* (larva) | 6.9-14.0 | 0.6 | 3.2725 | 0.97 | 20 |
| *Gryllus* | 7.0-23.0 | 14.5 | 2.6319 | 0.88 | 24 |
| *Euschistus* | 8.9-14.0 | 6.6 | 2.8041 | 0.90 | 20 |
| *Oebalus* | 7.5-11.6 | 76.9 | 1.6334 | 0.83 | 20 |
| *Disonycha* | 6.0- 7.9 | 8.8 | 2.7496 | 0.95 | 20 |
| *Clubiona* | 4.3- 7.9 | 3.8 | 3.1804 | 0.96 | 20 |
| *Polygyra* | 5.2-10.8 | 28.9 | 3.0294 | 0.99 | 20 |

APPENDIX 2
DIET OF GREEN TREEFROG

Prey identified from the stomachs of 163 *Hyla cinerea*. L = larva

| Prey Item | Total No. of items | Est. Biomass (g) | No. of Frogs | Adjusted *%BO* |
|---|---|---|---|---|
| Insecta | | | | |
| Coleoptera | 158 | 2.766 | 105 | 21.56 |
| Alleculidae | 21 | 0.356 | 5 | 1.91 |
| Cantharidae (L) | 46 | 0.793 | 32 | 7.21 |
| Cantharidae | 2 | 0.048 | 2 | 0.45 |
| Carabidae | 6 | 0.124 | 5 | 1.13 |
| Cerambycidae | 3 | 0.130 | 3 | 0.90 |
| Chrysomelidae | 27 | 0.387 | 15 | 3.45 |
| Curculionidae | 26 | 0.239 | 21 | 3.21 |
| Elateridae | 1 | 0.016 | 1 | 0.19 |
| Hydrophilidae | 1 | 0.002 | 1 | 0.06 |
| Languriidae | 8 | 0.307 | 6 | 1.94 |
| Scarabaeidae | 6 | 0.235 | 3 | 1.20 |
| Staphylinidae | 2 | 0.035 | 2 | 0.38 |
| Tenbrionidae | 1 | 0.094 | 1 | 0.44 |
| Unknown | 8 | - | 8 | - |
| Collembola | 21 | - | 13 | - |
| Dermaptera | 6 | 0.059 | 6 | 0.75 |

APPENDIX 2. Continued.

| Prey Item | Total No. of items | Est. Biomass (g) | No. of Frogs | Adjusted *%BO* |
|---|---|---|---|---|
| Insecta | | | | |
| Diptera | 16 | 0.009 | 13 | 0.45 |
| Hemiptera | 49 | 1.161 | 41 | 8.73 |
| Alydidae | 1 | 0.050 | 1 | 0.32 |
| Coreidae | 1 | 0.095 | 1 | 0.44 |
| Lygaeidae | 2 | 0.015 | 1 | 0.17 |
| Pentatomidae | 37 | 0.806 | 30 | 7.04 |
| Reduviidae | 8 | 0.195 | 8 | 1.79 |
| Homoptera | 14 | 0.194 | 13 | 2.01 |
| Cicadellidae | 9 | 0.114 | 8 | 1.37 |
| Cercopidae | 1 | 0.055 | 1 | 0.33 |
| Flatidae | 1 | 0.025 | 1 | 0.22 |
| Unknown | 3 | - | 3 | - |
| Hymenoptera | 41 | 0.150 | 35 | 2.90 |
| Formicidae | 29 | 0.053 | 23 | 1.57 |
| Ichneumonidae | 3 | 0.088 | 3 | 0.73 |
| Platygasteridae | 1 | 0.0001 | 1 | 0.02 |
| Unknown | 8 | - | 8 | - |
| Lepidoptera | 128 | 8.223 | 104 | 36.99 |
| Gelechiidae | 3 | 0.007 | 1 | 0.12 |
| Geometridae | 6 | 0.269 | 5 | 1.63 |
| Noctuidae (L) | 66 | 6.402 | 54 | 26.61 |

APPENDIX 2. Continued.

| Prey Item | Total No. of items | Est. Biomass (g) | No. of Frogs | Adjusted %BO |
|---|---|---|---|---|
| Insecta | | | | |
| Lepidoptera | | | | |
| Noctuidae | 2 | 0.433 | 2 | 1.34 |
| Nolidae (L) | 2 | 0.006 | 1 | 0.12 |
| Psychidae (L) | 1 | 0.003 | 1 | 0.08 |
| Zygaenidae (L) | 4 | 0.029 | 2 | 0.34 |
| Unknown (L) | 31 | 0.569 | 25 | 5.30 |
| Unknown | 13 | 0.505 | 13 | 3.60 |
| Odonata | 1 | 0.109 | 1 | 0.41 |
| Orthoptera | 41 | 2.044 | 40 | 11.43 |
| Acrididae | 1 | 0.220 | 1 | 0.67 |
| Blattidae | 10 | 0.418 | 9 | 2.77 |
| Gryllidae | 14 | 1.041 | 14 | 5.46 |
| Tetrigidae | 6 | 0.352 | 6 | 2.08 |
| Tettigoniidae | 2 | 0.013 | 2 | 0.23 |
| Unknown | 8 | - | 8 | - |
| Thysanoptera | 3 | - | 3 | - |
| Unknown | 67 | - | 49 | - |
| Arachnida | | | | |
| Acarina | 55 | - | 5 | - |
| Araneae | 72 | 0.712 | 62 | 8.40 |
| Araneidae | 7 | 0.083 | 5 | 0.92 |

APPENDIX 2. Continued.

| Prey Item | Total No. of items | Est. Biomass (g) | No. of Frogs | Adjusted *%BO* |
|---|---|---|---|---|
| Arachnida | | | | |
| Araneae | | | | |
| Clubionidae | 23 | 0.168 | 19 | 2.56 |
| Dictynidae | 3 | 0.003 | 3 | 0.14 |
| Linphiidae | 2 | 0.006 | 2 | 0.16 |
| Lycosidae | 9 | 0.275 | 7 | 1.99 |
| Mimetidae | 1 | 0.001 | 1 | 0.05 |
| Pisauridae | 2 | 0.019 | 2 | 0.28 |
| Salticidae | 4 | 0.041 | 3 | 0.50 |
| Tetragnathidae | 3 | 0.025 | 3 | 0.39 |
| Unknown | 18 | 0.092 | 17 | 1.80 |
| Opiliones | 12 | 0.285 | 12 | 2.34 |
| Chilopoda | | | | |
| Lithobiomorpha | 1 | - | 1 | - |
| Crustacea | | | | |
| Isopoda | 4 | 0.035 | 4 | 0.47 |
| Gastropoda | | | | |
| Stylommatophora | 9 | 0.592 | 9 | 2.92 |
| Polygyridae | 8 | 0.526 | 8 | 2.94 |
| Unknown | 1 | 0.066 | 1 | 0.36 |
| Reptilia | | | | |
| Squamata | 1 | 0.252 | 1 | 0.64 |

APPENDIX 2. Continued.

| Prey Item | Total No. of items | Est. Biomass (g) | No. of Frogs | Adjusted *%BO* |
|---|---|---|---|---|
| Reptilia | | | | |
| Squamata | | | | |
| Iguanidae | 1 | 0.252 | 1 | 0.72 |
| Total (Order) | 699 | 16.592 | | 100.00 |
| Total (Family) | 513 | 16.095 | | 99.63 |

## APPENDIX 3
## PARAMETER ESTIMATES FOR LENGTH-WIDTH EQUATIONS

Logarithmic function model: $y = b + m\ln x$. Power function model: $y = bx^m$. Length and width are in mm. *Polygyra* width estimate = 0.652 × length (see Table 6).

| Genus | Model | $b$ | $m$ | $r$ | N |
|---|---|---|---|---|---|
| *Musca* | Log | -5.31470 | 4.04408 | 0.92 | 10 |
| *Spodoptera* (larva) | Power | 0.06713 | 1.22141 | 0.99 | 14 |
| *Chauliognathus* (larva) | Power | 0.20221 | 0.98155 | 0.99 | 9 |
| *Gryllus* | Power | 0.25731 | 1.04462 | 0.99 | 17 |
| *Euschistus* | Log | -16.64649 | 10.10852 | 0.80 | 10 |
| *Oebalus* | Power | 0.68178 | 0.84693 | 0.97 | 10 |
| *Disonycha* | Log | -3.88884 | 3.76397 | 0.85 | 10 |
| *Clubiona* | Power | 0.33842 | 0.96167 | 0.96 | 10 |
| *Polygyra* | - | - | - | - | - |

## LITERATURE CITED


Arnold SJ (1977) Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. Science 197:676-678

Blackith RM, Speight MCD (1974) Food and feeding habits of the frog *Rana temporaria* in bogland habitats in the west of Ireland. J Zool Lond 172:67-79

Borchers H-W, Burghagen H, Ewert J-P (1978) Key stimuli of prey for toads (*Bufo bufo* L.): configuration and movement patterns. J Comp Physiol 128:189-192

Bragg AN (1957) Some factors in the feeding of toads. Herpetologica 13:189-191

Brower LP, Brower J (1962) Investigations into mimicry. Nat Hist 71:8-19

Bury RB, Martin M (1973) Comparative studies on the distribution and foods of plethodontid salamanders in the redwood region of northern California. J Herpetol 7:331-335

Carrel JE, Eisner T (1974) Cantharidin: potent feeding deterrent to insects. Science 183:755-757

Chesson J (1978) Measuring preference in selective predation. Ecology 59:211-215

Clark RD (1974) Food habits of toads, genus *Bufo* (Amphibia: Bufonidae). Am Midl Nat 91:140-147

Cock MJW (1978) The assessment of preference. J Ani Ecol 47:805-816

Cody ML (1974) Optimization in ecology. Science 183:1156-1164

Cott HB (1940) Adaptive coloration in animals. Oxford University Press New York

Ellis JE, Wiens JA, Rodell CF, Anway JC (1976) A conceptual model of diet selection as an ecosystem process. J Theor Biol 60:93-108

Emlen JM (1966) The role of time and energy in food preference. Amer Natur 100:611-617

Estabrook GF, Dunham AE (1976) Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. Amer Natur 110:401-413

Ewert J-P (1968) Der einfluß von zwischenhirndefekten auf die visuomotorik im beute- und fluchtverhalten der erdkröte (*Bufo bufo* L.). Z Vergl Physiol 61:41-70

Ewert J-P (1970) Neural mechanisms of prey-catching and avoidance behavior in the toad (*Bufo bufo* L.). Brain Behav Evol 3:36-56

Ewert J-P (1974) The neural basis of visually guided behavior. Scient Am 230:33-42

Ewert J-P (1976) The visual system of the toad: behavioral and physiological studies on a pattern recognition system. In: Fite KV (ed) The amphibian visual system. Academic Press New York San Francisco London, pp 141-202

Ewert J-P, Burghagen H (1979) Configurational prey selection by *Bufo*, *Alytes*, *Bombina*, and *Hyla*. Brain Behav Evol 16:157-175

Ewert J-P, Kehl W (1978) Configurational prey selection by individual experience in the toad *Bufo bufo*. J Comp Physiol 126:105-114

Ewert J-P, Arend B, Becker V, Borchers HW (1979) Invariants in configurational prey selection by *Bufo bufo* (L.). Brain Behav Evol 16:38-51

Finkelstein D, Grüsser O-J (1965) Frog retina: detection of movement. Science 150:1050-1051

Freed AN (1980*a*) An adaptive advantage of basking behavior in an anuran amphibian. Physiol Zool 53:433-444

Freed AN (1980*b*) Prey selection and feeding behavior of the green treefrog (*Hyla cinerea*). Ecology 61:461-465

Gardner BT (1964) Hunger and sequential responses in the hunting behavior of salticid spiders. J Comp Physiol Psych 58:167-173

Heatwole H, Heatwole A (1968) Motivational aspects of feeding behavior in toads. Copeia 1968:692-698

Hedeen SE (1972) Food and feeding behavior of mink frogs, *Rana septentrionalis* Baird, in Minnesota. Am Midl Nat 88:291-300

Himstedt W (1967) Experimentelle analyse der optischen sinnesleistungen im beutefangverhalten der einheimischen urodelen. Zool Jb (Physiol) 73:281-320

Hughes RN (1979) Optimal diets under the energy maximization premise: the effects of recognition time and learning. Amer Natur 113:209-221

Ingle D (1968) Visual releasers of prey-catching behavior in frogs and toads. Brain Behav Evol 1:500-518

Ingle D (1971) Prey-catching behavior of anurans toward moving and stationary objects. Vision Res Suppl 3:447-456

Ingle D (1975) Focal attention in the frog: behavioral and physiological correlates. Science 188:1033-1035

Ingle D (1976) Behavioral correlates of central visual functions in anurans. In Llinás R, Precht W (eds) Frog neurobiology. Springer-Verlag New York, pp 435-451

Ingle D, Cook J (1977) The effect of viewing distance upon size preference of frogs for prey. Vision Res 17:1009-1013

Ingle D, McKinley D (1978) Effects of stimulus configuration on elicited prey-catching by the marine toad (*Bufo marinus*). Ani Behav 26:885-891

Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press New Haven Connecticut

Johnson BK, Christiansen JL (1976) The food and food habits of Blanchard's cricket frog, *Acris crepitans blanchardi* (Amphibia, Anura, Hylidae), in Iowa. J Herpetol 10:63-74

Johnson CR, Bury RB (1965) Food of the pacific treefrog, *Hyla regilla* Baird and Girard, in northern California. Herpetologica 21:56-58

Kilby JD (1945) A biological analysis of the food and feeding habits of two frogs, *Hyla cinerea cinerea* and *Rana pipiens sphenocephala*. Quart J Fla Acad Sci 8:71-104

Klimstra WD, Myers CW (1965) Foods of the toad, *Bufo woodhousei fowleri* Hinckley. Trans Ill St Acad Sci 58:11-26

Korschgen LJ, Baskett TS (1963) Foods of impoundment and stream-dwelling bullfrogs in Missouri. Herpetologica 19:89-99

Kramek WC (1972) Food of the frog *Rana septentrionalis* in New York. Copeia 1972:390-392

Labanick GM (1976) Prey availability, consumption, and selection in the cricket frog, *Acris crepitans*. J Herpetol 10:293-398

Legler JM, Sullivan L (1979) The application of stomach flushing to lizards and anurans. Herpetologica 35:107-110

Linzey DW (1967) Food of the leopard frog, *Rana p. pipiens*, in central New York. Herpetologica 23:11-17

Luthardt G, Roth G (1979*a*) The relationship between stimulus orientation and stimulus movement pattern in the prey catching behavior of *Salamandra salamandra*. Copeia 1979:442-447

Luthardt G, Roth G (1979*b*) The influence of prey experience on movement pattern preference in *Salamandra salamandra* (L.). Z. Tierpsychol 51:252-259

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Natur 100:603-609

Mardia KV (1972) Statistics of directional data. Academic Press London New York

Marten GG (1973) An optimization equation for predation. Ecology 54:92-101

Oplinger CS (1967) Food habits and feeding activity of recently transformed and adult *Hyla crucufer crucifer* Wied. Herpetologica 23:209-217

Pulliam HR (1974) On the theory of optimal diets. Amer Natur 108:59-74

Pulliam HR (1975) Diet optimization with nutrient constraints. Amer Natur 109:765-768

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Quart Rev Biol 52:137-154

Rapport DJ (1971) An optimization model of food selection. Amer Natur 105:575-587

Rapport DJ (1980) Optimal foraging for complementary resources. Amer Natur 116:324-346

Rapport DJ, Turner JE (1970) Determination of predator food preferences. J Theor Biol 26:365-372

Roth G (1976) Experimental analysis of the prey catching behavior of *Hydromantes italicus* Dunn (Amphibia, Plethodontidae). J Comp Physiol 109:47-58

Roth G (1978) The role of stimulus movement patterns in prey catching behavior of *Hydromantes genei* (Amphibia, Plethodontidae). J Comp Physiol 123:261-264

Schoener TW (1969) Models of optimal size for solitary predators. Amer Natur 103:277-313

Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecol Syst 2:369-404

Schürg-Pfeiffer E, Ewert J-P (1981) Investigation of neurons involved in the analysis of gestalt prey features in the frog *Rana temporaria*. J Comp Physiol 141:139-152

Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill New York Toronto London

Sih A (1979) Optimal diet: the relative importance of the parameters. Amer Natur 113:460-463

Stenseth NC, Hansson L (1979) Optimal food selection: a graphic model. Amer Natur 113:373-389

Sweetman HL (1944) Food habits and molting in the common treefrog. Am Midl Nat 32:491-501

Toft CA (1980) Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. Oecologia 45:131-141

Turner FB (1959) An analysis of the feeding habits of *Rana p. pretiosa* in Yellowstone Park, Wyoming. Am Midl Nat 61:403-413

Tyler JD, Hoestenbach RD (1979) Differences in food of bullfrogs (*Rana catesbeiana*) from pond and stream habitats in southwestern Oklahoma. S W Nat 24:33-38

Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052

Zug GR, Zug PB (1979) The marine toad, *Bufo marinus*: a natural history resumé of native populations. Smith Contr Zool 284:1-58

## BIOGRAPHICAL SKETCH

On 14 March 1952, Arthur Nelson Freed was born in the city of brotherly love. His formative years were spent on the streets of Philadelphia and in the woods of Fairmont Park (the largest city park in the world). He graduated from Northeast High School but decided not to enter Temple University (considered by many to be Northeast's 13th grade). Instead, he headed west to study biology at Indiana University of Pennsylvania (Pennsylvania's largest state owned university). After four glorious years in the mountains of west-central Pennsylvania, Arthur returned to Philadelphia with one blue Alfa Romeo 1750 Spider Veloce and a B.S. in biology. He entered the Intern Teaching Program for College Graduates at Temple University (it was his destiny) and after two years earned an M.Ed. During those two years, he experienced the tragic loss of a Porsche 911E Targa, but bravely continued teaching seventh grade life science at Upper Moreland Junior High School, Upper Moreland, PA. He then decided not to devote his life to educating children, bought a Lotus Elan Sprint, and headed with élan south to the University of Florida in pursuit of the elusive Ph.D. He was half-heartedly accepted into the zoology graduate program, not being offered support until his second year. After two frustrating and three invigorating years he finally reached the top of the graduate student pecking order and tried vainly to apply for tenure. Seeing no hope of attaining *Nirvana*, he threw up his hands in disgust, and graduated.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Martha L. Crump

M. L. Crump, Chairperson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Anderson

J. F. Anderson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

T. J. Walker

T. J. Walker
Professor of Entomology and Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1982

Dean for Graduate Studies
and Research

UNIVERSITY OF FLORIDA
3 1262 08553 4294